

# A VOLUTID SPECIES RADIATION FROM NORTHERN HONDURAS, WITH NOTES ON THE HONDURAN CALOOSAHATCHIAN SECONDARY RELICT POCKET

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*Abstract.*—A previously unknown species radiation of the relict Neogene volutid genus *Falsilyria* has been found to exist in a secondary relict pocket along northern Honduras. Three new species, *Falsilyria garciai*, *F. kotorai*, and *F. retemirabilis* are described and the living species of the genus are reviewed. An hypothesis is proposed, taking into account Pleistocene glacially-induced sea level fluctuations, as an explanation for the existence of five sibling species on the Honduran continental shelf and offshore banks. The relict nature of the Honduran gastropod fauna is discussed and its affinities to the fauna of the Pinecrest Beds Formation of the Pliocene Caloosahatchian Province of South Florida are outlined.

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## Introduction

The Caribbean Molluscan Province has recently been shown (Petuch 1981; Petuch, in press) to be composed of an array of discrete faunas, each differing in both species composition and geological age. Since the Caribbean region actually consists of a faunal mosaic in both time and space, I referred to this type of zoogeographical pattern as geographical heterochrony (Petuch, in press). In that study, the geographically heterochronous Caribbean was shown to contain two types of anachronistic faunas. I referred to these zoogeographical subunits as relict pockets. In turn, these isolate small areas were seen to be geographically interspersed within a matrix of wide-ranging, recently evolved species.

One type of relict pocket was discovered in the Gulf of Venezuela region (Petuch 1981) and contained a fauna that closely resembled, in both generic and species compositions, the molluscan assemblages of Pliocene Caribbean formations such as the Gurabo, Bowden, Gatun, and Mare. This type was referred to as a primary relict pocket. Another type of relict pocket was discovered in the Yucatan, Mexico and Roatan Island, Honduras areas and contained few relict species but many relict genera. This type was referred to as a secondary relict pocket. In essence, relict pockets represent areas where evolution and extinction have been greatly slowed or stopped and have resulted in intact Neogene faunas that are “frozen” in time.

The shallow water (0–50 m) areas off northern Honduras, from near Roatan Island to the Nicaragua border, contain many extant elements of the Neogene Caloosahatchian Molluscan Province (Petuch, in press). Here, a

number of relict genera and species complexes have managed to survive and have undergone secondary speciation. These include the endemic Caloosahatchian genera *Cypraeorbis* (Cypraeidae), *Heilprinia* (Fasciolaridae), *Pleioptygma* (Mitridae), and *Falsilyria* (Volutidae), and complexes centered around several Caloosahatchian species. These will be discussed in detail later in this paper. I refer, collectively, to both the Northern Honduras continental shelf and bank areas and the area of the Yucatan Banks as the Caloosahatchian Secondary Relict Pockets.

The genus *Falsilyria* is a common and conspicuous component of the molluscan assemblages comprising the Honduran Caloosahatchian Secondary Relict Pocket. The genus first appears in the upper Eocene Inglis Limestone of Florida (S. Hoerle and E. Vokes 1978:106–107), where it is represented by two species. Probably an offshoot of *Lyria* s.s., *Falsilyria* was restricted to the Caloosahatchian Molluscan Province and evolved into five species by the lower Miocene. The evolution of the morphological characteristics of the genus, as a whole, parallel those of the genus *Voluta* of the Gatunian Province (S. Hoerle and E. Vokes 1978:107; Petuch 1980:117; Petuch, in press). There is a conspicuous gap, however, from the middle Miocene to the Recent, in which no known species of *Falsilyria* have been found in the fossil record.

*Falsilyria* was originally thought to be represented in the Recent by a single species, *F. demarcoi* (Olsson, 1965) (S. Hoerle and E. Vokes 1978:107). In 1980, however, I described a second living species, *F. morrisoni* (Petuch, 1980:115–117), from the north coast of Roatan Island. Since then, through the efforts of two active amateur malacologists, Dr. Emilio Garcia and Mr. Louis Kotora, I acquired a number of unusual forms of *Falsilyria*. These had been taken by commercial shrimp boats working along the Honduras coast and offshore banks. From the large suite of specimens, I found that there were actually several living *Falsilyria* species and that these represented a previously unknown species radiation or complex that was restricted to the confines of the refugium.

This paper gives a review of the living species of the genus, the descriptions of three new species and offers suggestions for patterns of evolution and speciation trends that can occur within secondary relict pockets. Specimens designated with USNM numbers are in the collection of the Division of Mollusks, National Museum of Natural History, Smithsonian Institution.

## Systematic Section

### Class Gastropoda

### Order Caenogastropoda

### Superfamily Volutacea Rafinesque, 1815

### Family Volutidae Rafinesque, 1815

### Subfamily Volutinae Rafinesque, 1815



Genus *Falsilyria* Pilsbry and Olsson, 1954

*Falsilyria* Pilsbry and Olsson, 1954:21.

*Type-species*.—*Lyria pycnopleura* Gardner, 1937, by original designation.

*Diagnosis*.—"Similar to *Voluta* Linné but with a narrower shell and higher spire; nucleus relatively small, consisting of but one (to two plus) rather loosely coiled whorls; sculpture formed by strong, smooth, nearly straight axial ribs, generally somewhat noded or coronated at the suture and with faint spirals showing around the base and on the canal; aperture semi-elliptical, the outer lip thickened by the last rib, smooth within; plaits on the columella and parietal wall are similar to those of *Voluta*; of these the four or five lower ones form large, strong, sharp folds which spiral deeply into the interior while above them the plaits on the parietal wall are small and weak; end of pillar appressed and turned sharply backwards to form a recurved beak forming a deep, siphonal notch; siphonal fasciole short but strong" (Pilsbry and Olsson 1954).

*Diagnosis by Olsson 1965*.—"Similar to *Voluta* in shape and parietal and columellar plaits, but distinguished by the constricted ends of the axial riblets bordering the suture. Sculpture of axial riblets smooth or crossed by encircling spirals."

*Remarks*.—Descriptions of fossil species of *Falsilyria*, together with a discussion on the evolution of the genus, were given by Hoerle and Vokes (1978:106–107, 120–128). The geographical range of the genus was discussed by myself (1980:117), as were the morphological relationships between the known Recent and fossil species.

*Falsilyria demarcoi* (Olsson, 1965)

Figs. 5–7, 24, 25

*Voluta demarcoi* Olsson, 1965:662–663, pl. 81, figs. 7, 7a, pl. 82, figs. 1, 1a, 1b, 1c.

*Falsilyria demarcoi*.—Hoerle and Vokes, 1978:107.—Petuch, 1980:115–116, figs. 9, 10.

*Material examined*.—Length 70 mm, trawled by commercial shrimpers from 15 m depth off north coast of Roatan Island, Honduras, 1979, USNM 784646; length 45 mm, trawled by shrimpers, 35 m depth off Roatan Island, Honduras, February 1980, USNM 784645; lengths 52 mm, 56 mm, 85 mm, trawled by commercial shrimp trawlers from 35 m depth south of the Caratasca Cays, north coast of Honduras, collection of Dr. Emilio Garcia, Lafayette, Louisiana; length 54 mm, trawled by shrimpers from 35 m depth off north coast of Roatan Island, Honduras, 1979, collection of Dr. Geerat J. Vermeij, University of Maryland.

*Distribution*.—From the area around Roatan Island, Honduras, to the Honduras-Nicaragua border in depths from 2–50 m.



Figs. 1-8. Species of *Falsilyria*: 1, *F. morrisoni*, dorsal aspect of holotype (USNM 784485), length 73 mm; 2, *F. morrisoni*, ventral aspect of holotype; 3, *F. garciai*, dorsal aspect of holotype, length 71 mm; 4, *F. garciai*, ventral aspect of holotype; 5, *F. demarcoi*, dorsal aspect of specimen from Roatan Island, length 54 mm; 6, *F. demarcoi*, dorsal aspect of specimen from Roatan Island (USNM 784645), length 45 mm; 7, *F. demarcoi*, ventral aspect of same specimen; 8, *F. morrisoni*, ventral aspect of paratype (USNM 784486), length 45 mm.



*Discussion.*—Although Olsson designated the type-locality of *F. demarcoi* as “. . . about 105 miles off Mezquitil, Texas, in 100 fathoms” (Olsson 1965:663), this is apparently in error. Neither this species nor any other member of the genus has been collected anywhere along the east coast of Mexico and Yucatan Banks, even though these areas are heavily fished at several depths by commercial shrimpers. The other locality given in the same paper, “. . . 5 fathoms (mud), Punta Patuca, Honduras” (Olsson 1965:663), appears correct and falls within the typical geographical and depth ranges of the species. The commercial shrimpers work the entire east coast of Central America from Yucatan south to Nicaragua and specimens of mollusks that are saved by the captains are often actually from several different localities. Since locality data on many of these specimens are sketchy or non-existent, it is not surprising that Olsson was misled in the geographical range of his new species. Unfortunately, these incorrect locality data have been carried on in the works of Weaver and duPont (1970:7), Hoerle and Vokes (1978:107), and others.

*Falsilyria demarcoi* has the widest distribution of the genus and it appears to range all along the mainland and the continental shelf of Honduras. Figure 24 shows a specimen of an unusually colorful population from the area near the Caratasca Cays. The specimen in Figs. 6 and 7 represents a dwarfed, but otherwise typically colored, individual from shallow water near Roatan Island.

*Falsilyria garciai*, new species

Figs. 3, 4

*Material examined.*—Holotype: Length 71 mm, width 34 mm, trawled by commercial shrimp boats from 35 m depth on Gorda Bank, off north coast of Honduras, 1980, USNM 784641. Paratype: Length 63 mm, same depth and locality as holotype, collection of Dr. Emilio Garcia, Lafayette, Louisiana.

*Shell description.*—Shiny, polished; body heavy, with 5 whorls; body whorl with 10 rounded axial ribs; all whorls with numerous sharply-defined minor axial ribs; anterior  $\frac{1}{4}$  of shell with 7 large, raised, beaded cords; shoulder sharply defined, strongly coronated; spire high, scalariform; spire whorls coronated, heavily sculptured with 7 large, raised, beaded cords; 3 cords on shoulder, enhancing coronated appearance; protoconch glassy, composed of 3 whorls; aperture narrow, roughly  $\frac{3}{5}$  of shell length; columella with 9 sharp-edged plications; base shell color cream-orange with 2 bands of deep purple-blue and sky-blue blotches, one band around midbody, one around anterior end; base color overlaid with numerous longitudinal dark brown zigzag flammules, some running entire length of shell; shoulder with scattered patches of dark brown dots; spire whorls blue-gray with radiating,

fine, dark brown zigzag lines that cross over raised spiral cords, giving them speckled appearance; protoconch tan; interior of aperture flesh-pink; columellar region orange, becoming darker at anterior end.

*Type-locality*.—35 m depth on Gorda Bank, Honduras.

*Distribution*.—At present, known only from Gorda Bank.

*Etymology*.—Named for Dr. Emilio Garcia, Lafayette, Louisiana, who first recognized the species as new and who has kindly donated the type and a large series of Honduran mollusks for study.

*Discussion*.—Of the known species of *Falsilyria*, both living and fossil, *F. garciai* is the only species with a color pattern of zigzag flammules. The sharp-angled shoulder coronations and the heavily sculptured spire whorls are closer to those of *F. morrisoni* than to those of any of the other living species. Unfortunately, the type-specimens both have thin lips, and judging from this thinness, probably represent subadult specimens. The rarity of this new species reflects the lack of extensive collecting on Gorda Bank. Future work in that area may bring to light more specimens of this distinctive volute.

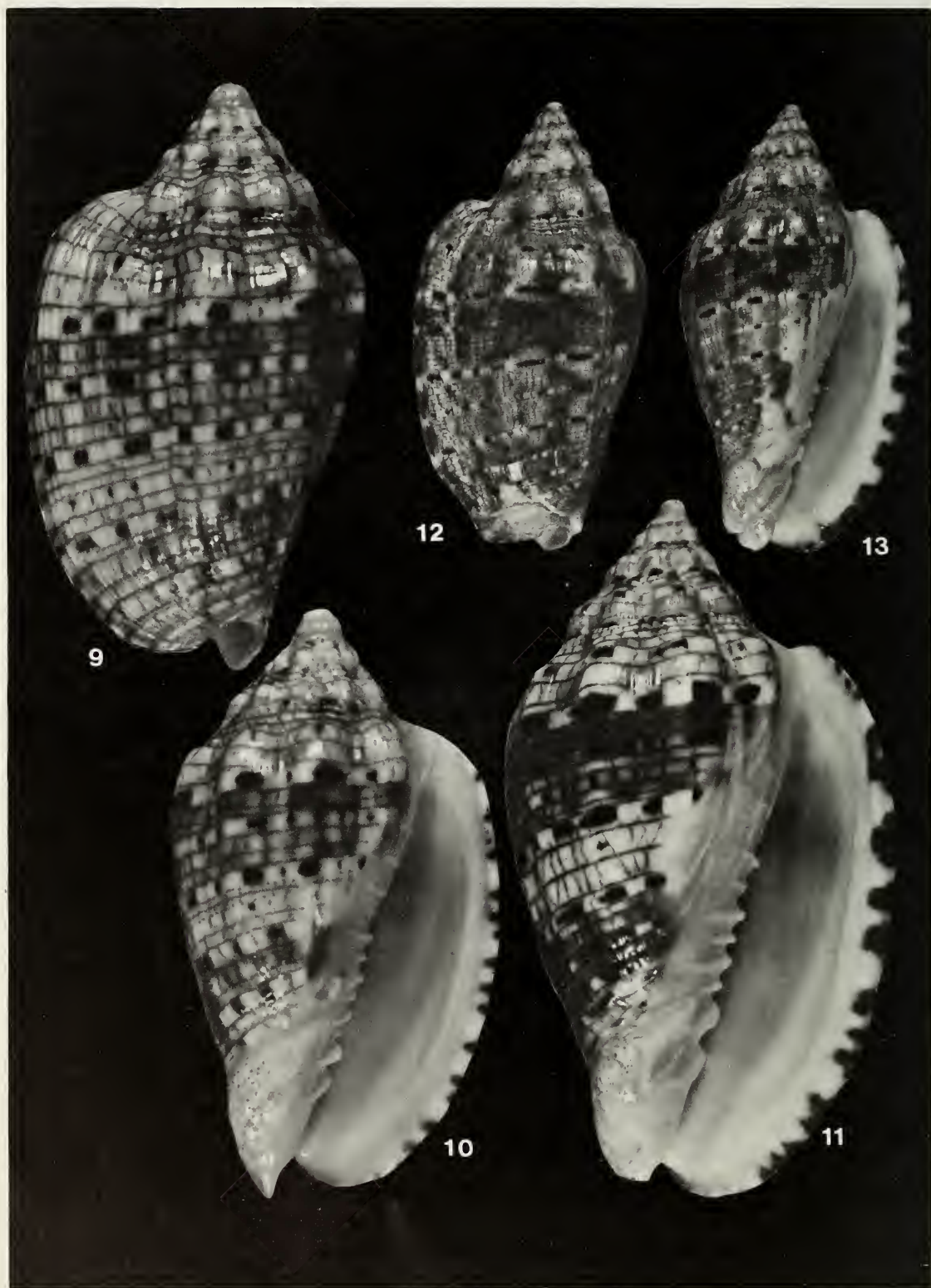
*Falsilyria kotorai*, new species

Figs. 9–11

*Material examined*.—Holotype: Length 49 mm, width 27 mm, brought up in lobster trap, occupied by hermit crab, from 36 m depth on Rosalind Bank, Honduras, January 1980, USNM 784642. Paratypes: Length 81 mm, same depth, locality, and date as holotype, USNM 784644; length 48 mm, same locality, collection of Dr. Emilio Garcia, Lafayette, Louisiana; length 76 mm, same depth, locality, and date as holotype, collection of Mr. Louis Kotora, St. Petersburg, Florida.

*Shell description*.—Shiny, polished; body heavy, thickened, with 4–5 whorls; body whorl with 7–10 rounded axial ribs; last whorl with numerous sharply-defined minor axial ribs towards edge of lip; spire low, roughly  $\frac{1}{4}$ – $\frac{1}{5}$  total shell length; spire whorls with 3 undulating, beaded spiral cords; protoconch very large for genus, with 3 bulbous whorls; aperture large, wide, lenticular, roughly  $\frac{3}{4}$  of total shell length; columella with 12–14 thin, smooth, sharp-edged plications; lip thickened and flaring in adults; base shell color bright salmon-pink with 2 wide bands of wine-red and purple blotches, one band posterior to midbody line, one anterior; base color overlaid with 5–7 evenly-spaced revolving bands of black and white spots and secondary system of numerous evenly-spaced revolving brown lines connected by short, staggered, longitudinal lines, producing “brick wall” pattern; protoconch white at tip, turning to orange; interior of aperture salmon-pink, becoming orange towards edge of lip; edge of lip white with numerous black spots; columella orange, with white plications.





Figs. 9–13. Species of *Falsilyria*: 9, *F. kotorai*, dorsal aspect of holotype, length 49 mm; 10, *F. kotorai*, ventral aspect of holotype; 11, *F. kotorai*, ventral aspect of paratype (USNM 784644), length 81 mm; 12, *F. retimirabilis*, dorsal aspect of holotype, length 75 mm; 13, *F. retimirabilis*, ventral aspect of holotype.

*Type-locality*.—36 m depth on Rosalind Bank, Honduras.

*Distribution*.—At present, known only from Rosalind Bank.

*Etymology*.—Named for Mr. Louis Kotora, St. Petersburg, Florida, who first recognized the species as new and who kindly donated the type material.

*Discussion*.—Of the four other known Recent species of *Falsilyria*, the new species most closely resembles *F. demarcoi* and *F. retemirabilis*, n. sp. *Falsilyria kotorai* differs from *F. demarcoi* in having a lower spire, larger protoconch in proportion to shell size, and in lacking both the bright orange-peach base color and bands of fine brown specklings that are characteristic of Olsson's species. *Falsilyria kotorai* differs from *F. retemirabilis* in having a red and pink shell color, in having a coarse "brick" pattern instead of a fine "net" pattern, and in having a larger protoconch.

*Falsilyria morrisoni* Petuch, 1980

Figs. 1, 2, 8

*Falsilyria morrisoni* Petuch, 1980:115–117, figs. 1–6.

*Material examined*.—Lengths 73.4 mm (holotype) and 45.4 mm (paratype), 60 m depth off north coast of Roatan Island, Honduras, January, 1979, USNM 784485 (holotype) and 784486 (paratype); length 42 mm, same depth and locality as holotype, collection of Dr. Emilio Garcia, Lafayette, Louisiana.

*Distribution*.—At present, known only from off Roatan Island.

*Discussion*.—*Falsilyria morrisoni* is the only known living species to have beaded columellar plications (Petuch 1980:fig. 5). In having this character, *F. morrisoni* most closely resembles the fossil *F. mansfieldi* (Dall, 1916) and may be the direct descendant.

*Falsilyria retemirabilis*, new species

Figs. 12, 13

*Material examined*.—Holotype: Length 75 mm, width 38 mm, trawled by commercial shrimp boats from 20 m depth off Caratasca Cays, Honduras, November, 1980, USNM 784643.

*Shell description*.—Shiny, highly polished; body thick, heavy, with 5 whorls; body whorl smooth, with 11 low, flattened axial ribs; anterior  $\frac{1}{4}$  shell with 4 wide, raised spiral cords; shoulder rounded, smooth; spire high; early spire whorls heavily sculptured with raised spiral threads, later whorls smooth; 3 slightly raised spiral threads on last spire whorl; protoconch glassy, composed of 3 whorls; aperture large, flaring, roughly  $\frac{3}{4}$  total shell length; columella with 15 plications, 5 of which are larger than others; base shell color cream-yellow with 2 continuous bands of blue-gray, one above



midbody line, one at anterior end; base shell color overlaid with numerous intermeshing, horizontally and vertically-oriented rows of tiny brown dots which form a fine net pattern over entire shell; net pattern, in turn, overlaid by 10 wide, revolving bands of alternating dark brown and violet-blue dashes; protoconch white at tip, turning orange; interior of aperture flesh-colored; columella cream-yellow with white plications.

*Type-locality*.—20 m depth off Caratasca Cays, Honduras.

*Distribution*.—At present, known only from the area near the Caratasca Cays.

*Etymology*.—From the Latin “rete,” net, and “mirabilis,” wonderful; in reference to the fine net pattern that is characteristic of this new species.

*Discussion*.—Unfortunately, this new species is known only from the holotype. The remarkable net pattern of *F. retemirabilis*, however, is unique among the known Atlantic Volutidae, setting it aside from all other members of the genus. Besides color pattern, the protoconch of *F. retemirabilis* differs from that of *F. demarcoi* in being larger and more bulbous. It is not as large, however, as that of *F. kotorai*, and is intermediate in form. The rarity of *F. retemirabilis*, like that of *F. garciai*, is again probably a direct result of the lack of collecting on the Honduran offshore banks.

### Comparison of the Shell Morphologies of the Living *Falsilyria* Species

*Color patterns*.—The color patterns of the five known living species of *Falsilyria* are of three basic types: 1, a pattern composed of two wide, continuous bands of fine spiral lines, one around the midbody, one around the anterior end, alternating with two spiral bands of fine speckles; 2, a pattern composed entirely of fine, continuous or dotted spiral lines connected by short vertical lines, producing a “brick wall” or “net” pattern; 3, a pattern composed primarily of zigzag vertical lines that run the length of the shell. All of these patterns, in turn, overlie an amorphous, secondary background pattern that is usually composed of large blotches of various colors or numerous spiral bands of large, dark dashes. In all, the various combinations of these distinctive patterns appear to be species specific. Even within the range of each species’ pattern, however, considerable variation exists. This is evidenced by the color morphs of *F. demarcoi*, shown here in Figs. 5–7 and 24, and those of *F. kotorai* (Figs. 9–11).

The first type of color pattern is found in both *F. demarcoi* and the fossil *F. anoptos* (Hoerle and Vokes, 1978:pl. 5, figs. 4c, 4d) and in a modified form in *F. morrisoni*. Details of the second type of pattern are shown here, for *F. kotorai* (Fig. 15) and *F. retemirabilis* (Fig. 16). This brick-net type of pattern is also found in Indo-Pacific volutids such as *Harpulina aurisiaca* (Lightfoot, 1786) and *Lyria cloveriana* Weaver, 1963. The brick-net pattern is in direct contrast to the elongated vertical flammules of *F. garciai* (Fig.



14



15



16

Figs. 14–16. Details of the color patterns of the three new *Falsilyria* species, traced from photographs. Magnification approximately 10 $\times$ . 14, *F. garciai*; 15, *F. kotorai*; 16, *F. retemirabilis*.

14). The zigzag pattern of *F. garciai* closely resembles the color pattern of the Brazilian *Voluta ebraea* Linnaeus, 1758, while the dotted band pattern of *F. demarcoi* and *F. morrisoni* is similar to that of the southern Caribbean *Voluta musica* Linnaeus, 1758.

All three types of color patterns are variations on a basic theme of fine spiral lines and dots and this is probably an ancestral morphological character for the whole genus. The similarity of color patterns between *Falsilyria* and *Voluta* most likely reflects a common ancestor for both genera (Hoerle and Vokes 1978:107; Petuch 1980:117). The retention of this ancestral color pattern may represent a trend towards morphological conservatism within both groups.



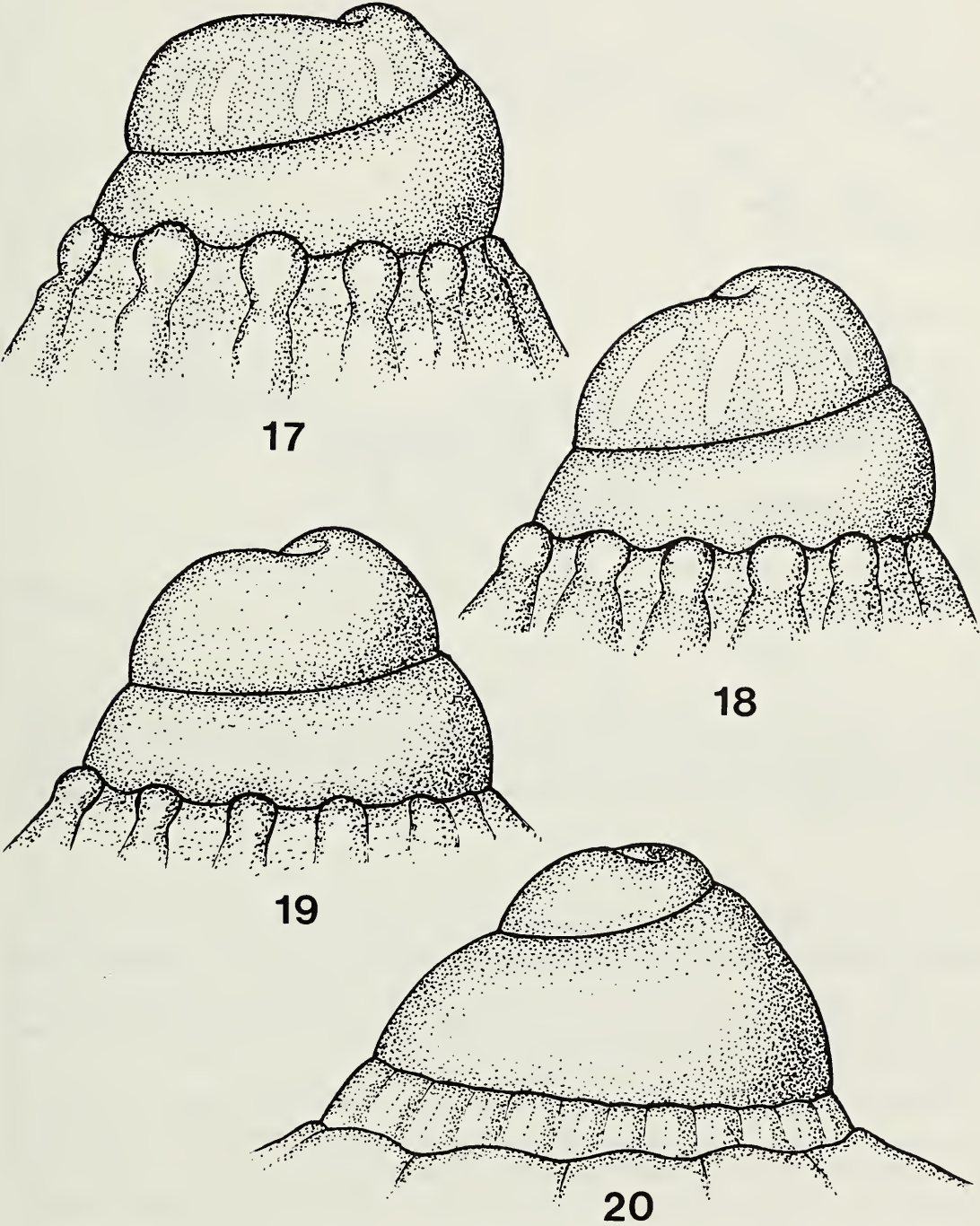
*Protoconchs*.—In the Volutidae, the protoconch is a powerful tool for species determinations. Since volutes undergo direct development, all embryonic stages take place within the egg capsule and eventually result in a crawl-away hatchling (Hyman 1967:306, 313). Environmental and physiological effects such as substrate type and diet do not affect the self-contained embryo as they would the adult shell. The protoconch, then, can be viewed as a direct genotypic indicator and not as a reflection of ecophenotypic variation.

Characteristically, all living *Falsilyria* species have protoconchs with  $2\frac{1}{2}$  whorls. The general form of the protoconchs of *Falsilyria* is quite different from that of the related genus *Voluta*. The protoconchs of *Falsilyria* differ in being smaller, cylindrical-shaped, and more exerted than those of *Voluta*. That genus can be seen to have protoconchs that are larger, broader, dome-shaped, and often ornamented with axial ribs. In having a smaller protoconch in proportion to total shell size, *Falsilyria* more closely resembles the genera *Lyria*, *Cordilyria*, *Enaeta*, and *Festilyria* than it does *Voluta*. Within this general form, however, two basic types of protoconchs can be discerned for the five living species.

The first type is found in *F. demarcoi*, *F. garciai*, and *F. retimirabilis*, and consists of the first and second nuclear whorls being roughly equal in size. This gives the protoconch a decidedly cylindrical appearance. In *F. demarcoi* (Fig. 19), the nuclear whorls are roughly parallel to the adult body whorl. On the other hand, both *F. garciai* (Fig. 17) and *F. retimirabilis* (Fig. 18) have nuclear whorls that are noticeably tilted to one side. This is especially obvious in *F. garciai*, which also has the first whorl flattened, producing a truncated appearance. This cylindrical-type protoconch is also found in the fossil *F. mansfieldi* (Dall, 1916) (S. Hoerle and E. Vokes 1978:pl. 5, figs. 4–5).

The second type of protoconch is found in *F. morrisoni* and *F. kotorai*. Although equally as exerted as the above-mentioned species, this type is more rounded, with the first whorl being smaller than the second (Fig. 20). Although differing greatly in shell shape and sculpture, *F. morrisoni* and *F. kotorai* have very similar protoconchs. The fossil *F. anoptos* also has a rounded protoconch (S. Hoerle and E. Vokes 1978:pl. 5, fig. 4e) and closely resembles that of *F. kotorai*.

The five living species can easily and consistently be separated by the shapes of their protoconchs. This was readily seen while examining several color forms of *F. demarcoi*. Although the shell coloration and size often differed greatly, the protoconchs were always identical in shape, size, and color. In *Falsilyria*, the two basic types of protoconchs occur throughout the geological range of the genus. There is no pattern to their occurrence and they do not appear to represent any type of derived or ancestral character state.



Figs. 17–20. Details of the protoconchs of four *Falsilyria* species. 17, *F. garciai*; 18, *F. retemirabilis*; 19, *F. demarcoi*; 20, *F. kotorai*.

Speciation Within a Secondary Relict Pocket

The pattern of speciation seen in *Falsilyria* appears to be the direct result of the separation of a wide-ranging ancestral stock into reproductively isolated gene pools. This separation was further reinforced by subsequent bar-





Fig. 21. Map of the Recent northwestern Caribbean Sea, showing the range of the Honduran Caloosahatchian Second Relict Pocket. RI—Roatan Island; C—Caratasca Cays; G—Gorda Bank; R—Rosalind Bank; S—Serranilla Bank. The banks can be seen to be separated by wide channels.

riers to dispersal of all the isolates. This is a classic example of a vicariance zoogeographic pattern and is one that is more commonly seen in insular terrestrial organisms. The topography of the Honduran Caloosahatchian Secondary Relict Pocket, however, produces an analogous island biogeographic pattern in a marine situation.

The area of the Caloosahatchian refugium is characterized by a series of adjacent, shallow water banks that are separated by wide, deep water channels (Fig. 21). These present barriers to dispersal for shallow water organisms that lack planktonic larvae. The effectiveness of these channel barriers varied greatly during the Pleistocene and depended, primarily, on high or low water stands during glacial and interglacial periods. During an extreme low water stand, such as one of minus 100 m in the mid-Pleistocene (CLIMAP members 1976:1131–1133; Emiliani 1971:183–197), the entire Honduran continental shelf, including the deep channels and bank regions, was exposed (Olsson 1972:120). During a high water stand, such as during the Sangamonian Interglacial Period, the Caribbean flooded the shelf and the shallow banks were again separated by deep, impassable channels.



Fig. 22. Reconstruction of the Caribbean coastline during a peak Pleistocene low water stand, superimposed upon the outline of the Recent coast of Central America. Shading indicates the hypothetical range of the ancestral *Falsilyria* stock (after Petuch, in press).

The combination of a bank-channel topography and multiple glacial sea level fluctuations had a tremendous effect on the speciation and extinction of organisms such as *Falsilyria*. Being shallow water animals, with no species living much below 50 m depth, and also being animals with non-planktonic crawl-away young, *Falsilyria* was especially susceptible to reproductive isolation. In an attempt to explain the existence of five sibling species occurring within the same relict pocket, I here outline an hypothesis that involves a three-step speciation mechanism.

1. With an extreme sea level drop during a peak glacial period (CLIMAP members 1976:1137), the Honduran and Nicaraguan continental shelves were exposed. This resulted in a long continuous coastline bordering a steep drop-off. In the shallow water area, an ancestral *Falsilyria* stock could range along this entire coast with no barriers to reproduction or dispersal. A reconstruction of the Caribbean coastline during a Pleistocene low water stand and the hypothetical range of *Falsilyria* at that time are both given in Fig. 22.

2. With the advent of an interglacial period, sea levels began to rise, separating, one after the other, the various component banks along the



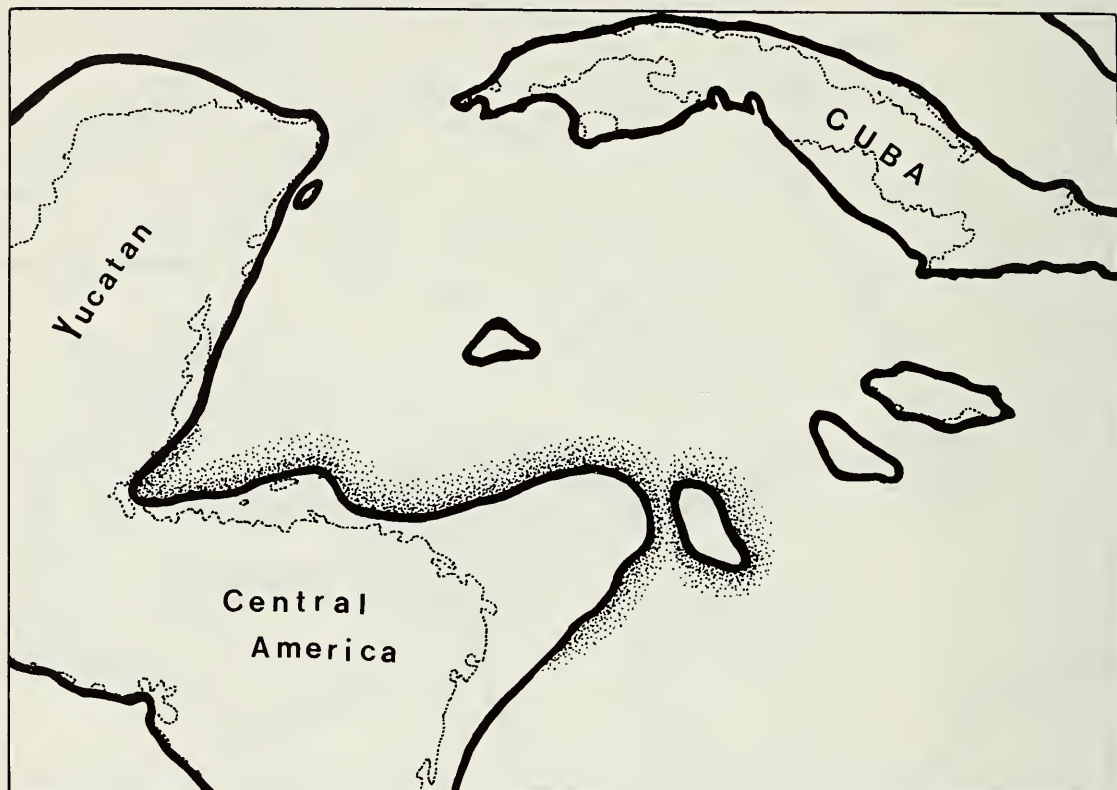


Fig. 23. Reconstruction of the Caribbean coastline at the beginning of an interglacial period, superimposed upon the outline of the Recent coast of Central America. Shading indicates the hypothetical range of the ancestral *Falsilyria* stock. This stage marks the beginning of isolation of the shallow banks by intervening deep channels (after Petuch, in press).

continental shelf. Due to its position at the end of the platform, the Rosalind-Serranilla Bank complex was probably among the first to separate from the fused mainland shelf and banks. A deep channel formed between this bank and the continental shelf, causing the bank population of *Falsilyria* to become isolated from the mainland stock. The sectioning of the once-continuous coastline and the isolation of a bank fauna are both shown in Fig. 23.

3. During full interglacial periods, such as at present, the Honduran continental shelf and offshore banks contained a series of shallow water areas (less than 35 m), each with its resident, non-dispersing population of *Falsilyria*. Over time, and together with the selection pressures caused by sea level fluctuations, these isolates would attain full species status. The reinvansion of *Falsilyria* onto the post-glacially flooded continental shelf would also set the stage for speciation by allowing a radiation into a variety of open niches. Together, these two formats would allow for allopatric speciation.

Considering that the Caribbean region was subject to at least ten major sea level fluctuations during the Pleistocene (CLIMAP members 1976; Em-

iliani 1971), it is not surprising that there are five sibling species of *Falsilyria* within the relict pocket. Three species are absolutely allopatric, with *F. garciai* apparently being confined to the Gorda Banks, *F. retimirabilis* to the Caratasca Cays, and *F. kotorai* to the outlying Rosalind Bank. Only *F. demarcoi* ranges along the entire continental shelf and is sympatric with *F. morrisoni* off Roatan Island and possibly Utila Island. The outermost bank, Serranilla Bank, most probably has a resident endemic species, but this area has yet to be sampled. Future work may turn up other endemic species when the smaller banks near Gorda Bank are sampled.

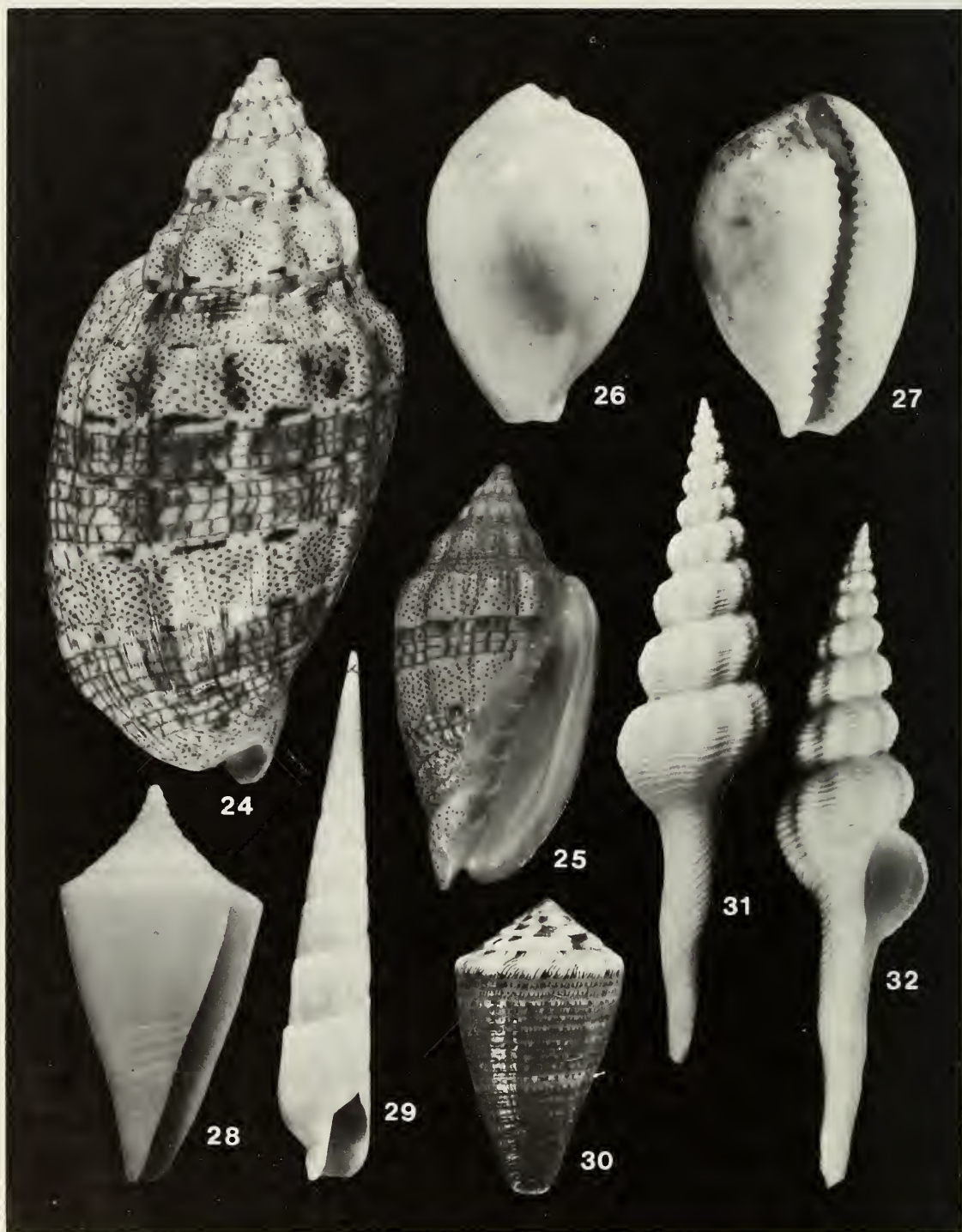
### Characteristics of the Honduran Caloosahatchian Relict Gastropod Fauna

Coexisting with the *Falsilyria* species radiation are large numbers of other relict gastropod groups that, together with the volutes, give the refugium an archaic appearance. Most of these genera are also known to have crawl-away young and appear to have paralleled the same speciation pattern seen in the *Falsilyria* radiation. On the other hand, some groups have diverged only slightly from their ancestors in the Pliocene Pinecrest Beds Formation of South Florida.

Adding a Pliocene flavor to the relict pocket are several endemic Caloosahatchian genera and species complexes. Some of these relicts, such as *Pleioptygma* (*P. helenae* (Radwin and Bibbey, 1977)), *Heilprinia* (*H. dowianus* (Olsson, 1954)), and *Turbinella scolymoides* (Dall, 1890), have previously been discussed by myself (1980:115) and E. Vokes (1966:63). Since then, several other archaic groups have been collected. These included the first known living *Cypraeorbis* (Cypraeidae), a large *Ficus* in the *Ficus caloosahatchiensis* (B. Smith, 1907) species group (Ficidae), a large undescribed *Heilprinia*, several new *Conus* species (Conidae), an unusual *Myurellina* (Terebridae), members of the *Oliva carolinensis* Conrad, 1840 complex (Olividae), an apparent *Hindsiclava* (Turridae) species radiation, and trochid-like archaeogastropods that are probably referable to the "extinct" family Colloniidae.

A single specimen of a large (length 45 mm, width 30 mm) *Cypraeorbis* species (Figs. 26, 27) was taken in 1966 by the University of Miami R/V *Pillsbury*, at station P-598, near the northern end of the relict pocket. This undescribed species closely resembles *Cypraeorbis willcoxi* (Dall, 1890) from the Miocene Chipola Formation of North Florida, in both shape and size and also labial dentition. The North Florida Miocene influence is also present in the Conidae, with an undescribed 16 mm species of *Conus* (USNM 784647) (Fig. 28) from the Gorda Bank that closely resembles *C. rapunculus* S. Hoerle, 1976 from the Alum Bluff Group (S. Hoerle 1976:pl. 4, fig. 6). The Roatan Island endemic *Conus kulkulcan* Petuch, 1980 (USNM





Figs. 24–32. Species of *Falsilyria*, *Cypraeorbis*, *Conus*, *Myurellina*, and *Heilprinia*: 24, *Falsilyria demarcoi*, dorsal aspect of specimen from south of Caratasca Cays, length 85 mm; 25, *F. demarcoi*, ventral aspect of specimen from Roatan Island, length 53 mm; 26, *Cypraeorbis* sp., dorsal aspect of 45 mm specimen, P-598; 27, *Cypraeorbis* sp., ventral aspect of same specimen; 28, *Conus* sp., ventral aspect of specimen from Gorda Bank (USNM 784647), length 16 mm; 29, *Myurellina* sp., ventral aspect of specimen from Rosalind Bank, length 80 mm; 30, *Conus kulkulcan*, dorsal aspect of holotype (USNM 784487), length 21 mm; 31, *Heilprinia* sp., dorsal aspect of 190 mm specimen, P-602; 32, *Heilprinia* sp., ventral aspect of same specimen.

784487) (Fig. 30) may also be part of a Caloosahatchian relict stock that originated with the Chipolan *C. praecipuus* S. Hoerle, 1976 (S. Hoerle 1976:pl. 4, fig. 4). Besides the Honduran endemic *Heilprinia dowianus*, the relict genus *Heilprinia* is also represented by a large (190 mm) undescribed species (University of Miami, P-602) from near Rosalind Bank (Figs. 31, 32). In the same area, the Caloosahatchian genus *Myurellina* is represented by two relict pocket endemics, *M. stegeri* (Abbott, 1954) and a large (80 mm) undescribed species (Fig. 29).

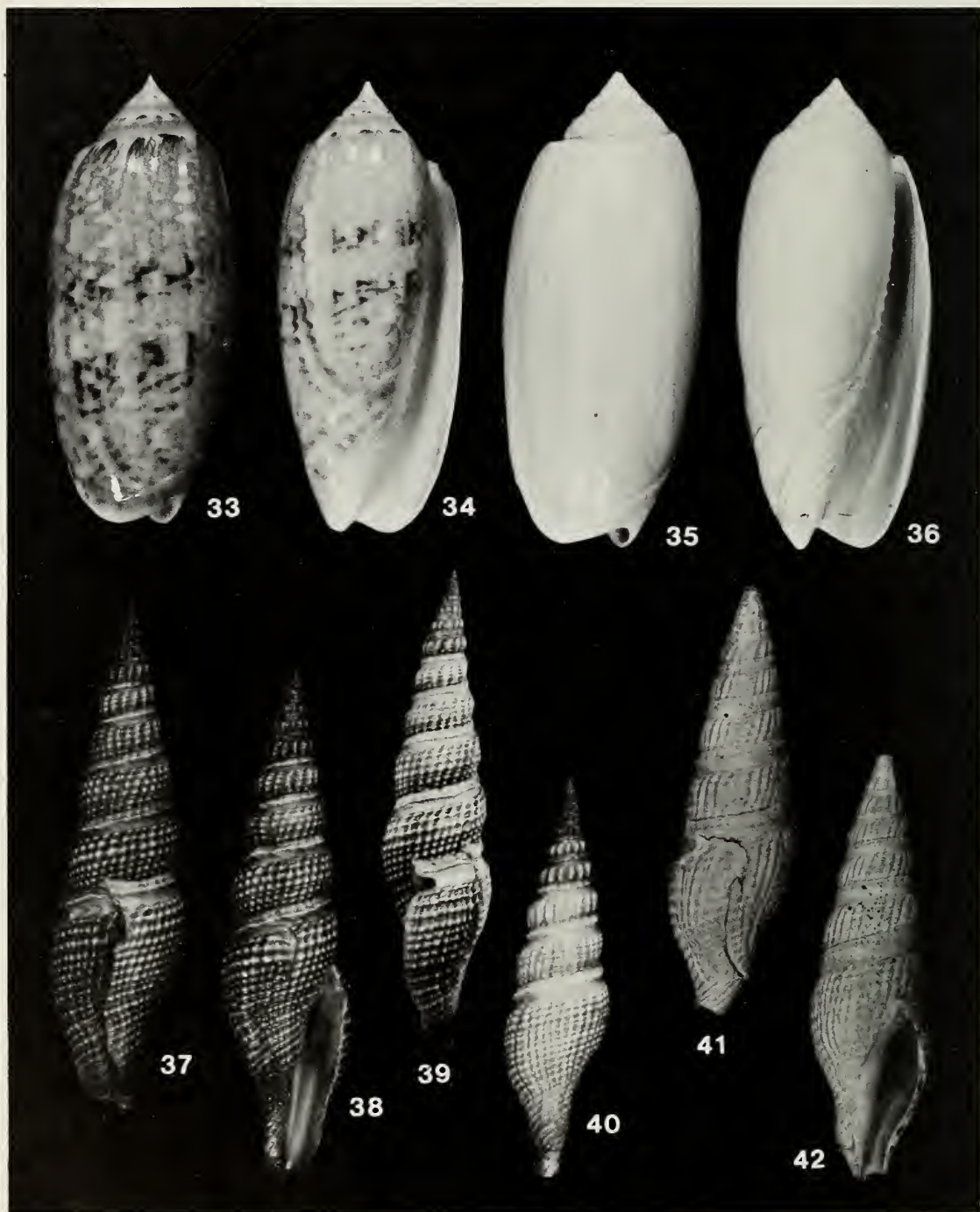
Faunal affinity to the Pliocene Pinecrest Beds Formation of South Florida is particularly striking in two groups of Honduran caenogastropods. A large *Oliva* species, found along the northern end of the pocket near Roatan Island, is nearly identical to *Oliva carolinensis*, both in size and shape. To illustrate this point, a 65 mm specimen of this species (USNM 784648) (Figs. 33, 34) is shown next to a 69 mm fossil *O. carolinensis* from the Pinecrest Beds Formation at Sarasota, Florida (Figs. 35, 36). Along with the relict *Oliva*, a complex of large *Hindsiclava* turrids has been found on the outer banks. One of these, from Rosalind Bank, closely resembles the middle Pliocene *Hindsiclava perspirata* (Dall, 1890). For comparison, a 70 mm specimen (USNM 784649) (Figs. 37–39) and a 55 mm specimen (USNM 784649) (Fig. 40) of this large turrid are illustrated next to a 61 mm fossil specimen of *H. perspirata* from the Pinecrest formation at Sarasota, Florida (Figs. 41, 42). As can be seen, both the *Oliva* and the *Hindsiclava* closely resemble their Floridian ancestors.

### Discussion

The speciation pattern in *Falsilyria* is also found in the Volutidae of other secondary relict pockets around the world. Some of the best examples are found in the Flindersian Secondary Relict Pockets of South and West Australia (Petuch, in press). Here, the relict Mio-Pliocene genera *Cottonia*, *Ericusa*, *Notopeplum*, *Notovoluta*, *Paramoria*, and *Pterospira*, have also survived into the Recent and have undergone secondary speciation. Other examples of relict volutes that have undergone reradiation after reduction of their original ranges are seen in the genera *Minicymbiola*, *Odontocymbiola*, and *Weaveria*, of the Platensian Relict Pocket (Petuch, in press) of Southern Brazil and Uruguay, and the genus *Athleta* (*Volutocorbis*) of Southeast Africa and the Mozambique channel.

Within the scheme of geographical heterochrony, the Caloosahatchian Secondary Relict Pockets, together, represent a temporal midpoint between the Recent Caribbean molluscan fauna and the intact Neogene fauna of the Gatunian Primary Relict Pocket in Venezuela. The glacial sea level fluctuations, with the accompanying alternating faunal separations and meldings, did not affect the Honduras area as much as they did the Florida Peninsula. This allowed a Mio-Pliocene Florida-type fauna to continue into the Recent





Figs. 33–42. Species of *Oliva* and *Hindsiclava*: 33, *Oliva* cf. *carolinensis*, dorsal aspect of specimen from north of Roatan Island (USNM 784648), length 65 mm; 34, *Oliva* cf. *carolinensis*, ventral aspect of same specimen; 35, *Oliva carolinensis*, dorsal aspect of fossil from Pinecrest Beds Formation, length 69 mm; 36, *Oliva carolinensis*, ventral aspect of same specimen; 37, *Hindsiclava* sp., dorsal aspect of specimen from Rosalind Bank (USNM 784649), length 70 mm; 38, *Hindsiclava* sp., ventral aspect of same specimen; 39, *Hindsiclava* sp., lateral aspect of same specimen showing anal notch; 40, *Hindsiclava* sp., dorsal aspect of specimen from Rosalind Bank (USNM 784649), length 55 mm; 41, *Hindsiclava perspirata*, dorsal aspect of fossil specimen from Pinecrest Beds Formation, length 61 mm; 42, *Hindsiclava perspirata*, ventral aspect of same specimen.

Caribbean, but in an altered state due to secondary speciation. With the exception of the living Pliocene fauna of the unevolved Gatunian Primary Relict Pocket, the rest of the Caribbean has evolved a new post-Pleistocene fauna that is considered the provincial indicator (Petuch, in press).

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